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Some remarks on the classification of the family *Hymenolepididae* Fuhrmann, 1907 *(Cestoda)*

Uwagi o systematyce rodziny *Hymenolepididae* Fuhrmann, 1907 (*Cestoda*)

Examining the tapeworms of small mammals (Rybicka, 1959) I met with several problems connected with their classification, in particular, those of the family *Hymenolepididae* Fuhrmann, 1907. The classification of this family has not yet been satisfactorily completed, in spite of several attempts at revision.

Since an increasing number of authors (Cohn, 1901; Clerc, 1902; Fuhrmann, 1907; Mayhew, 1925; Lopez-Neyra, 1942; Skrjabin et Mathevossian, 1945, 1948; Spassky, 1954; Spassky et Spasskaja, 1954) have attempted to work out a system which would depict the phylogenetic relations between tapeworms and introduce their proper taxonomy, it might be useful to add some remarks based on my own investigations. A new opinion in this field is to be found in the paper by Spassky (1954) on the classification of *Hymenolepididae* of mammals, and in the paper by Spassky and Spasskaja (1954) discussing *Hymenolepididae* of birds.

The first of these has been accepted by the Polish parasitologists (Żarnowski, 1955; Pojmańska, 1957; Sołtys, 1957; Kisielewska, 1958) and therefore I should like to deal with this problem first of all.

My studies on the tapeworms of mammals have led me to make certain reservations with regard to Spassky's (1954) conception, and therefore I cannot accept his taxonomy (Rybicka, 1959).

A very characteristic feature in Spassky's classification is the isolation of a great number of new monotypic genera. Within *Hy-*

menolepididae of mammals, Spassky distinguishes 19 genera, leaving 10 species without precise generic assignment as *Hymenolepis* s. l. Thirteen of the 19 above-mentioned genera are monotypic, two of them — *Neoskrjabinolepis* and *Vigisolepis* — comprise two species each, and only 4 genera comprise 7 — 15 species.

It should be stressed that in a given group of animals there may exist numerous monotypic genera. However, in my opinion, the designation of new genera must be based on equivalent criteria, while in Spassky's work various criteria are used. In certain cases, the main characteristic is the armature of the suckers (*Armadolepis*) in others, the general type of scolex structure, i. e. the hypertrophic tissue among the suckers (*Cryptocotylepsis*) and in another case, the

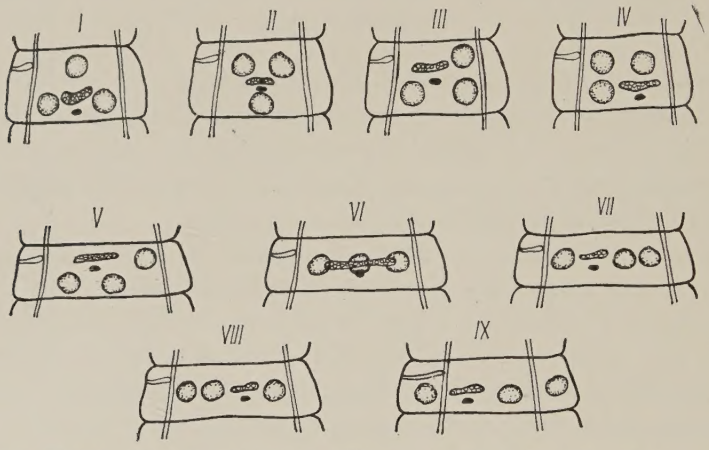

Fig. 1. Types of testes pattern — after Skrjabin et Matevossian, 1945.*

splitting up of the strobila into fragments, which in turn develop independently in the bowel of the host (*Gvosdevilepis*) etc.

In the 15 cases mentioned above, the diagnosis of the genera is the same as the diagnosis of the species. Some of Spassky's descriptions of the genera are based on an incomplete description of the species, while a more exact examination of the species may indi-

* During the print of present paper there appeared the notice of Spassky: Spassky A.A. — Utočnienie klassifikacji topografičeskich otnošenii polovych organov gimenolepidid. Zool. Žurn., 38, 1, 1959. In that notice the author gives more types of testes pattern. I will omit them because these new conceptions do not change my further considerations.

cate that there are no characters suggesting the existence of a separate genus. As an example, the case of the genus *Myotolepis* (Spassky, 1954) may be given, where the genus was recognised on the basis of an incomplete description of *Dicranotaenia crimensis* Skarbilovitsch, 1946, already discusser in detail by Żarnowski (1955). In other cases the description of the genus is based on the structure of one particular species and does not correspond to the description of another species attributed to this genus. This is particularly noticeable in the description of the genus *Neoskrjabinolepis* Spassky, 1947. The description is based on the structure of the species *Neoskrjabinolepis schaldybini* Spassky, 1947, considered by Żarnowski (1955) and by Rybicka (1959) as conspecific with *Hymenolepis singularis* Cholodkovsky, 1912 — a single species which can be assigned to the genus *Neoskrjabinolepis*. On the basis of my own work and of data from literature, I may state that the structure of *Hymenolepis singularis* Cholodkovsky, 1912 does not correspond to the description of the genus *Neoskrjabinolepis* Spassky, 1947.

The characters of the genus giving rise to doubts are:

(1) The arrangement of the testes in one line, whereas, according to Baer (1932) the arrangement of the testes of *H. singularis* can be triangular if there is muscular relaxation and elongation of the segments.

(2) The position of the female genital glands in the middle of the segment — in the specimens I have examined — the yolk gland always had an antiporal position. (Unfortunately, not all authors describe the position of this organ, therefore it is difficult for me to ascertain, if the particular case I mentioned, was not an exception).

(3) The serial structure of the strobila. In *H. singularis* this was shown for the first time in a drawing by Sołtys (1952), but it was not stressed in the description. Judging from the material I have examined (apart from my own material I also had that collected by Pojmańska, 1957), the structure of the strobila of *H. singularis* cannot be regarded as being serial. I suppose that even in the work of Sołtys the serial structure is marked only because the drawing is very schematic.

It should be stressed that Kobulej (1953) in his work published after the year 1947 (that is after Spassky drew attention to this character) states that he did not observe a serial type of structure

in *H. singularis*, and Żarnowski (1955) stresses that a serial structure does not appear in all specimens.

Another example is found in the differentiation of the genus *Soricinia* Spassky et Spasskaja (1954), based on one species *Hymenolepis soricis* Baer, 1928. The diagnosis of the genus, dealing among other things with the type of testes arrangement, coincides with the diagnosis of the species. Therefore the species *Hymenolepis tripartita*, found later (Żarnowski, 1955), though very similar to *H. sorcis* and differing only in the testes arrangement, should not be included in the genus *Soricinia*, and Żarnowski (1955) in attempting to show the similarity of these species, had to change the diagnosis of the genus.

As the diagnosis of genera given by Spassky are very limited, many species are left as *Hymenolepis* s. l.

According to my observations *Hymenolepis muris-sylvatici* (Rudolphi, 1819) belongs to such species. In my opinion the list of these species should be enlarged by the inclusion of *Hymenolepis stefańskii* Żarnowski, 1954 later included by Żarnowski (1955) in *Vampirolepis*. *Vampirolepis* Spassky, 1954 comprises species with numerous segments, while in the case of *H. stefańskii* the number of segments appears to be 7—12, which is exceptionally small.

The structure of the strobila of the genus *Vampirolepis* is not of a serial type — each segment is slightly more developed than the previous one, while in *H. stefańskii* after some mature segments there suddenly appear the gravid segments.

The hooks of *H. stefańskii* have not the wide guard typical for the genus *Vampirolepis*. As in Spassky's system there is no genus which contains species similar to *H. stefańskii*; this species remains in that scheme as belonging to *Hymenolepis* s. l.

A more detailed analysis of the taxonomical characters of Spassky's system, can be made by means of examination of genera including several species, i. e. *Rodentolepis* Spassky, 1954, *Staphylocystis* Villot, 1877 (Spassky, 1950) and *Vampirolepis* Spassky, 1954. Table I presents a summary of the taxonomical characters of these genera, based on the description of Spassky (1954).

Discussing the differentiation of the genus *Rodentolepis*, Spassky (1954) gives the morphological characters typical for the species classified, the arrangement of the testes according to type VII and the presence of one crown of hooks of the fraternoidal type.

Table I

Genus	*Rodentolepis* Spassky, 1954	*Staphylocystis* Villot, 1877	*Vampirolepis* Spassky, 1954
Definitive host	*Rodentia, Primates, Insectivora*	*Insectivora, Chiroptera*	*Chiroptera, Insectivora, Marsupialia, Passeres*
Intermediate host	*Arthropoda*, or no intermediate host	*Arthropoda*	probably *Arthropoda*
No. of hooks	more than 10	more than 10	numerous — up to 50
Shape of hooks	fraternoid	fraternoid — blade and guard of equal length	fraternoid — wide guard equal to the length of blade
Type of testes pattern*	V, VII	III	VI
Internal seminal vesicle	present	present	present
Ovary	in the middle of the segment	lobe-like	
Uterus	sack-like	sack-like	sack-like
Muscles	more than 4 belts	more than 4 belts	numerous
Excretory system	2 pairs	typical	

* Types of testes pattern = see Fig. 1.

„Since the uniformity in the structure of scolex and strobila are in this case accentuated by the common habitat, we are inclined to consider this group of organisms as a whole and from the phylogenic, i. e. systematic standpoint, put it into a separate genus *Rodentolepis* Spassky, 1954" (Spassky, 1954).

Species having the same single crown of hooks of the fraternoid type and the testes arrangement according to type III are classified to the genus *Staphylocystis* Villot, 1877. Species very similar to the above mentioned genus, but having the testes arrangement according to the pattern VI are classified to a third genus, *Vampirolepis* Spassky, 1954. In all these three cases one of the factors deciding the differentiation of a new genus was the attempt to take into account

the biological characteristics of the species considered here and therefore, first of all, their host-groups.

And so species of the genus *Rodentolepis* parasitize mainly *Rodentia, Staphylocystis - Insectivora* and *Vampirolepis - Chiroptera.*

It appeared, however, after taking into consideration the morphological taxonomical characters given by Spassky that morphological differences cannot be distinctly correlated with host-groups, consequently the species of each of the three genera parasitize various hosts. And so the attempt to form a system based on the biology of species under examination was not realized. On the other hand analizing the morphological differences shown in the description of genera we can observe a considerable similarity in all characters, and a single distinct differential character in the type of testes pattern.

The problem of the variability of this character of the tapeworms and the fact that it cannot be considered as a taxonomical feature has been discussed by several students. Dubinina (1953) and Rybicka (1958) have their reservations as to the recognition of the genus *Dicranotaenia* by Skrjabin et Mathevossian (1954) based on the type of testes pattern. Żarnowski (1955) draws attention to the fact that this character because of its considerable variability cannot be regarded as a good taxonomic character and showed that in the specimens he examined there was greater variability of testes patterns in the species belonging to the three genera in question, than that described by Spassky. At the same time Żarnowski revised Spassky's diagnosis of the genera. Table II gives the comparison of diagnostic characters of the three genera in question (Żarnowski's amendments being taken into account).

Table II

Genus	*Rodentolepis* Spassky, 1954	*Staphylocystis* Villot, 1877	*Vampirolepis* Spassky, 1954
Definitive host	*Rodentia, Primates*	*Insectivora, Chiroptera*	*Chiroptera, Insectivora*
Intermediate host	appears or not	*Arthropoda*	unknown
Number of hooks	more than 10	more than 10	up to 50
Shape of hooks	fraternoid	fraternoid	fraternoid
Type of testes pattern	I, III, V, VII	I, II, II, V	VI

Table II shows that according to Żarnowski (1955) these three genera are divided into two groups according to their biological habitat (or: according to their hosts). One of them is the genus *Rodentolepis* including species parazitizing *Rodentia* and *Primates*, the other includes *Staphylocystis* and *Vampirolepis* parazitizing *Insectivora* and *Chiroptera*. On the other hand, the type of testes pattern which, according to Spassky is the essential character differentiating the genus, exhibits such considerable variability, that it cannot be regarded as a diagnostic character and a basis for division into these two groups. In the second group, in order to recognize the genera *Staphylocystis* and *Vampirolepis*, Żarnowski accepts the type of testes pattern as the differentiating character, pointing out that in the case of pattern VI (*Vampirolepis*) this character shows considerable stability. However it should be mentioned that in the drawing of *Vampirolepis ruodabushi* (Macy et Rausch, 1946) given by Spassky, we can see in the neighbouring segments the type VI testes pattern as well as type VII. Spassky (1954) writes also, that the hooks of *Vampirolepis* have a characteristic wide guard while the same type of hook structure is found in *Hymenolepis furcata* Stieda, 1819 which is included in the genus *Staphylocystis*. Spassky (1954) as well as Żarnowski (1955) both stress that the classification of the genus *Vampirolepis* is only tentative.

Taking into consideration the above mentioned similarity between the genera of the second group (*Staphylocystis* and *Vampirolepis*) it seems that it would be more reasonable to consider them congeneric including here species of testes types I, II, III, V, VI, VII, parazitizing *Insectivora* and *Chiroptera*. It appears that the differences between the species recorded as belonging to genus *Rodentolepis* on the one hand, and *Staphylocystis* and *Vampirolepis* on the other, are limited only to the biological differences (their occurrence in different hosts).

This however gives rise to the problem whether or not such differences can be considered as diagnostic characters of a genus. There are numerous cases among tapeworms where the species of one distinct genus parasitize various hosts. For instance, the genus *Choanotaenia* can be found in various families of birds and mammals, *Diorchis* in various families of birds. *Rodentia* and *Insectivora* are not parasitized by the same species of tapeworms. On the other hand, as is shown by the above remarks — we find here species of considerable morphological similarity belonging to *Rodentolepis* and *Staphylocystis* genera. These observations show that in the cases in question —

as the result of adaptation to the environment (host) speciation could take place. At the same time the considerable morphological similarity among species parazitizing *Rodentia* and *Insectivora* points to their phylogenetic relationship. Therefore it seems more correct to consider such morphologically similar species as belonging to one genus, which in this case would include the genera *Rodentolepis* Spassky, 1954, *Staphylocystis* Villot, 1877 and *Vampirolepis* Spassky, 1954. A more detailed analysis of the morphology and biology of all these species may of course prove, that some of them should be eliminated from this genus, as for example *Hymenolepis stefańskii* Żarnowski, 1954 which in my opinion is incorrectly classified to the genus *Vampirolepis*.

After the division of the original genus *Hymenolepis* into several new genera, Spassky unites some of them into a new suprageneric category — the *Ditestolepea* "tribe" (supergenus). It seems that the „tribe" should include genera showing a more distinct phylogenetic relationship with one another than with other genera. They should have more basic similarity, than secondary characteristics due to adaptation.

Spassky describes the *Ditestolepea* "tribe" as "*Hymenolepididae* the strobila of which consists of series of segments clearly differing in their degree of maturity, provided that within one series the segments are equally developed" (Spassky, 1954) and he includes here the genera *Ditestolepis* Sołtys, 1952, *Neoskrjabinolepis* Spassky, 1947, *Protogynella* Jones, 1943, and *Soricinia* Spassky et Spasskaja, 1954.

The four genera mentioned above (in general comprising one species) show considerable differences in the structure of the strobila. The diagnosis of the "tribe" *Ditestelopea* is undoubtedly in harmony with that of *Ditestolepis diaphana* (Cholodkovsky, 1906) and *Soricinia tripartita* Żarnowski, 1955. Both these species have a distinct division of the strobila into three parts containing segments equally developed, with the same tendency for the whole part with the gravid segments to fall off. In none of these species did I observe the confluence of the uterus, which confirms the observations of Żarnowski (1955) contrary to the data of Sołtys (1952) concerning *D. diaphana*. On the other hand I did not observe a distinct serial type of strobila structure of *Hymenolepis (Neoskrjabinolepis) singularis* Cholodkovsky, 1912, according to the data of Kobulej (1953) and Żarnowski (1955). In the gravid seg-

ments of this species the confluence of the uterus does take place. It is possible that the whole gravid segments part can break away from the strobila, but it seems to have a completely different character, than in the case of the species mentioned above.

The type of strobila structure of *Protogynella blarinae* Jones, 1943* closely resembles the species *Pseudodiorchis kampinosi* Rybicka, 1958. Because of the very small dimensions of the two species and the very short segments, the analysis of their internal morphology is particularly difficult, and that is the reason why I suggested (Rybicka, 1958) that these two species may be closely related, and the different description of their internal organs may be the result of the varied interpretation of both authors. However, regardless of the details of the anatomical structure of both these species as well as *H. singularis* they show continuous development of segments. The general shape of the strobila is distinctly compact, the segments are short, and lie closely together, and do not tend to break away. Therefore we cannot speak here about the serial structure of strobila. The gravid segments of both species are filled gradually with maturing eggs. In the two or three last segments one can find mature eggs with well developed oncospheres. The boundary between these segments as well as between the uterus, becomes so indistinct that this can be compared to the confluence of the uterus appearing in *H. singularis*.

If we next examine the basic taxonomical characters which were also considered by Spassky, such as the presence or lack of rostellar hooks, their shape, number, and the number of testes, we see that the *Ditestolepea* „tribe" includes genera (or species) with completely different characters.

Ditestolepis and *Soricinia* have no rostellar hooks, yet the former has two testes, and the latter three. *Neoskrjabinolepis* has ten big hooks and three testes while in *Protygenella* there is a crown of numerous small hooks and one testis. In addition, this species is functionally proterogynous, which is very rare among tapeworms.

Treating the type of strobila structure of the *Ditestolepea* „tribe" as being a more important character (which as I have already said is not a uniform one) than such characters as the hooks or rumber of testes, does not seem to be correct since in all probability the hooks

* Since I could not obtain the original work of Jones (1943) I have used data given by Skrjabin et Mathevossian (1948), Spassky (1954), Wardle et Mc Leod (1952).

and testes are more primordial and durable features of tapeworms. This will be discussed in more detail below.

My remarks concerning the classification of S p a s s k y (1954) are connected mainly with the problems which I met with during the classification of my own material. They show that such a type of classification does not properly depict the phylogenetic relationships in the family *Hymenolepididae* and in many cases even makes them more obscure. In addition lack of equivalent criteria in the formation of a particular genera makes the classification of the material examined more difficult. Nearly all the species examined by me showed certain deviations and inconsistencies with the S p a s s k y descriptions of the genus, which make it necessary either to change description of the genus (which was done in many cases by Ż a r n o w s k i, 1955) or to form new genera for the species under examination.

It seems to me, that the acceptance of either, would increase the obscurity of the present system.

It also seems to me that it is still too early to form a new system of *Hymenolepididae* which would depict in the best possible way the phylogenic relations, first of all because of the lack of sufficient data on the biology of tapeworms and their ontogeny, research on which would undoubtedly contribute to the solving of this problem. On the other hand on the basis of our present knowledge it is already possible to discuss the problem as to which of the characters taken into account in the present taxonomy point to closer relationships among various species and which of them are of secondary importance. Therefore, without trying to make further generalizations, I should like to discuss pertinent observations which I have made during my work till now (R y b i c k a 1957a, 1957b, 1958a, 1958b, 1959).

First of all it is necessary to consider which of the morphological and biological characters may be an indication of phylogenetic relationship and which of them represent only specific modifications. Because of the lack of paleontological evidence the examination of the phylogeny of tapeworms is based on other data. A knowledge of their ontogenetic development might be very helpful, and research based on the biogenetic law of H a e c k e l and the earlier so-called law of B a e r, might help in the reconstruction of their phylogenic relationships. In connection with this, let us try to analyse the meaning and value of various morphological and biological characters of tapeworms from the standpoint of their ontogenetic development. It should be mentioned that even H a e c k e l himself stressed

that palingenetic and coenogenetic processes may be found in the ontogeny. Severcov (1949) in his theory of phylembriogenesis approches the matter from a different angle, distinguishing anaboly, deviations and archallaxis, which should be taken into consideration during any attempts to find a connection between the ontogeny of animals and their phylogeny.

My remarks mainly devoted to the family *Hymenolepididae* might appear onesided. I think however that in comparison with the data relating to other cestode groups and in the course of a broader discussion they might to some extent contribute to the explanation of several problems connected with the classification of tapeworms.

To begin with it is necessary to draw attention to the basic difference between the earliest larval form of *Cestoda* (oncosphere) and *Cestodaria* (lycophore). The oncosphere has always three pairs of embryonal hooks whereas the lycophore has five pairs of hooks. Ogren (1957) gives a comparative study of 7 types of hexacanth embryons (oncospheres) of tapeworms with the already known cytological structure. These types represent various groups of tapeworms (*Mesocestoidae, Taeniidae, Anoplocephalidae, Hymenolepididae, Linstowiidae, Proteocephalidae* and *Diphyllobothriidae*). Of course the differences between various oncospheres can be examined only on the basis of cytological methods, because purely morphological observations are not sufficient to make proper comparisons. The above mentioned examples show that basic differences in the earliest stages of development correspond to the taxonomic categories of tapeworms and so, according to the Baer law they are the indication of early phylogenetic differentiations into the main stocks.

The manner of development of the successive larval form — metacestode and its scolex pattern is one of the main criteria for the division of the tapeworm into orders. Differences in the scolex pattern, the first part of the future adult tapeworm, seem to be an essential indication of the relationship of various tapeworms.

The scolex of the members of the *Hymenolepis* family is characterised by the presence of four suckers and a rostellum with a crown of hooks in the majority of species. These hooks, because of their structure, are a stable feature, characteristic for particular species of tapeworm. Analizing the taxonomic importance of this feature we generally take into consideration the following points: (1) Presence or lack of hooks, (2) their shape, (3) size, (4) number. Their mode of de-

velopment should be also taken into consideration. Up to now studies have been made on this subject based on the examination of the cysticercus larvae (Leuckart, 1856, 1863; Gläser, 1908; Crusz, 1947, 1948; Dollfus, 1952), echinococcous (Goldschmidt, 1900), coenurus (Clapham, 1942), cysticercoid (Schmidt, 1894; Rybicka, 1957b).

In all the above mentioned cases a great number of hooklets were observed in the initial stage of development. Only part of these hooklets reached the final stage of development, and the rest disappeared. Since this has been observed among various types of larvae of *Cyclophyllidea* we can suppose that this is a primordial character. It is probable that among the mature tapeworms of this order the presence of a greater number of hooks (and therefore a smaller degree of their reduction in the course of development) means a more primitive character, than the final development of a small number of them. This seems to be proved by the fact that in species with more hooks there are more variations in number, while in those with a small number of hooks there is a considerable stability. Therefore a general treatment of the problem as to whether or not the number of hooks is a stable or varying character of tapeworms, as is given, for example, by Czapliński (1950) would not appear to be correct. *Hymenolepididae* can be divided according to that character into:

(1) Species without hooks, (2) species of a stable, small number of hooks (8, 10, 12) and (3) species of varying number of hooks (about 20, several dozen, or over 100).

It is important from the point of view of phylogenetic relations to ascertain whether hooks begin to form and then disappear in a later stage of development in all species without hooks, as was observed in *Hymenolepis erinacei* Gmelin, 1889 and *H. stendeneri* Janicki, 1904. The discovery of species deprived of the first traces of hooks in the ontogeny would indicate the existence of a separate stock in spite of the final coincidence of this feature (the lack of hooks in the adult stage).

The shape of the hooks is perhaps the most stable character of a species of the tapeworms. In some cases this feature in comparison with the testes number makes it possible to define clearly the genus, as for instance *Aploparaxis* Clerc, 1903 or *Diorchis* Clerc, 1903. The size of the hooks, however, varies in each particular species and can be considered as individual variations. In the great majority of coses, however, these differences are a matter of a few microns.

Yet there exist cases when we meet considerable differences in the size of hooks (e. g., *Hymenolepis singularis* Cholodkowsky, 1912). It is a common species, identified always in the same way by various authors. An exception is the isolation of the second species *Neoskrjabinolepis schaldybini* Spassky, 1947 considered by other authors (Żarnowski, 1955; Rybicka, 1959) as a synonym of *H. singularis*. This species has a very characteristic shape of hook and its dimensions vary from 35-62 μ. Continual variability does not occur here and a certain series of specimens can be found with relatively smal variations of the hook dimensions, such as 35—40 μ, 42—46 μ, 55—57 μ, or 58—62 μ. As I had the opportunity of comparing various series I may state that these differences are not the result of the various methods of measurement used by various authors. Czapliński (1956) mentioning similar cases of considerable variation in the dimensions of the hooks of *Diorchis flavescens* (Krefft, 1871) or *Hymenolepis microsoma* (Creplin, 1829) comes to the conclusion that this data requires confirmation, since there exists a possibility that the authors examined various species of the tapeworms. It is probable that a more detailed examination of the structure of *H. singularis* will show that it represents a group including various species, but up to now, even the attempts to isolate these two types according to their hosts (Żarnowski, 1955) apper to be unsuccessful (Rybicka, 1959).

In discussing the elements of the scolex, it is necessary to mention its interesting modification appearing in *Vigisolepis spinulosa* Cholodkovsky, 1906. In this species, apart from the crown of hooks at the top of the rostellum, there are elongated belts of small hooklets on its neck. This character, very specific, distinctly shaped and developing already in the ontogeny can be considered — in the light of the analysis of characters already discussed — as an early phylogenetic differentiation. Therefore I considered that Mathevossian (1945) was justufied in including this species in a separate genus *Vigisolepis* (Rybicka, 1959).

Besides the presence of hooks, the armature of the suckers or the lack of it is a characteristic feature of the scolex structure. It is a primitive feature appearing already in the larval development. The barbs on the suckers are, like the hooks, one of the few permanent elements in the structure of a tapeworm. The armature of the suckers may be considered as an essential feature from the taxonomic and phylogenetic point of view. We should remember, however, that this

feature may be examined only on the basis of some knowledge of larval structure, since in the case of adult tapeworms the hooks very often fall out and their lack may lead to incorrect conclusions. This problem I have already discussed in the study of species from the genus *Diorchis* Clerc, 1903 (Rybicka, 1957a).

In the definitive host, i. e., at the last stage of the development of the tapeworm, a strobila is formed containing the whole reproductive system. The structure of the reproductive system is, besides the hooks, the second basic taxonomical criterion. In the great majority of species the phenomenon of proandria occurs and may be that is why the testes as an early developing element are one of the most stable characters of the species.

In the description of particular species, their number, size, shape and position are taken into consideration. As far as the testes number is concerned we are faced with the same problem as in the case of hooks. With one, two or three testes per segment these numbers are always stable and characteristic for a given species. This made it possible to isolate such species as *Aploparaxis* Clerc, 1903 (one testis) or *Diorchis* Clerc, 1903 (two testes). Yet with an increase in the testes number it appers to vary in various segments of the same specimen. It is necessary to take into account, that even in species of *Hymenolepididae* with three testes we meet cases where the number of testes is changed in some segments, as for instance *Hymenolepis asymmetrica* Janicki, 1904 (Pojmańska, 1957) or *H. muris-sylvatici* (Rudolphi, 1819) (Rybicka, 1959).

In species having differences in the testes number in various segments, there are also considerable variations in the testes pattern. The problem of various types of testes pattern among *Hymenolepididae* was studied especially by Skrjabin et Mathevossian (1945) and accepted as one of the basic criteria for the classification of a genus. The same criterion was observed by Spassky in his classification of *Hymenolepididae* (Spassky, 1954; Spassky et Spasskaja, 1954). This criterion, however, has been questioned many times (Dubinina, 1953; Żarnowski, 1955; Rybicka, 1958a, 1959) and the criticism appears to be justified, Żarnowski (1955), however, pointed out that some types of testes pattern have a certain stability.

It seems that in the variability of types of testes pattern it is necessary to distinguish two different phenomena:

(1) The difference in the type of testes arrangement in various segments of one specimen, and (2) differences appearing among various specimens of one species. In the first case we can speak about the lack of stability of this feature, characteristic for a given species, in the second about the differentiation of various forms within one species.

The size and shape of testes belong undoubtedly to the characters of considerable variability, depending first of all on the degree of development of particular segments.

The organ which exhibits a considerable stability of structure is the cirrus. Its structure is often disregarded in descriptions of the species, may be because it is not always well preserved in preparation. A detailed study of the structure of the three species of the genus *Diorchis* C l e r c, 1903 (R y b i c k a, 1957a) which are undoubtedly closely related, shows distinct specific differences in the structure of this organ. Thus it seems that this character has no particular phylogenetic importance, while in practice, in the course of species classification it may be considered as an important taxonomical feature.

The female reproductive organs (the ovary, yolk gland) appearing in older segments, have in general a constant position in various species, and there is a certain variability of the shape of particular segments, connected with the degree of their development.

It should be stressed however that the general type of structure of the ovary and yolk gland (lobe-like, spherical) is generally stable within a species.

The structure of the uterus is distincly different for various families of tapeworms (the presence or lack of uterine porus, a branched-, or sack-like uterus) while such characters as the confluence of the uterus in the neighbour segments, or breaking away of parts of gravid segments, found in *Hymenolepididae* rather seem to indicate a secondary adaptation of various species arising under the influence of the environment. It is necessary to remember that these features appear in species which are not closely related (as stated above) but which are similar in the small dimensions of the whole strobila, a character which is undoubtedly connected with life in a definite ecological niche, such as the bowels of *Insectivora*. In species such as *Pseudodiorchis kampinosi* R y b i c k a, 1958 or *Protogynella blarinae* J o n e s, 1943 the mature eggs are so big that they cannot

find enough room in the very narrow limits of one segment. This might cause the breaking of barriers between the segments and in consequence lead to the confluence of the uterus of both segments. This character appears also in *Hymenolepis singularis* Cholodkovsky, 1912, a species undoubtedly different from the two mentioned above, but having a very similar segment structure which in effect could produce a similar type of uterus development. The remarks above dealt mainly with the most constant characters, easiest to measure and describe, and for that reason put foremost in the classification of the tapeworms.

Yet the characters which are more variable and more difficult to observe, should also be examined. For example the general shape of a given species of the tapeworm.

Differences of this type can be observed in the different shapes of the external egg shells, for instance the formation of long filaments characteristic for various species of the genus *Diorchis* (Rybicka, 1957a, b; Jarecka, 1958). In the structure of larvae a good example may be the difference in shape of the cercomeres of cysticercoids (ramicercus, microcercus, etc.). In the case of adult tapeworms it is, above all, the size of the tapeworm as well as the general shape of the scolex and segments. The size is of course a variable feature, as it shown in the experiments of Pavlovskij and Gnezdilov (1951). Yet it is necessary to remember that they were doing experimental work. In natural conditions a considerable variability of this character is also observed but in a limited sense. Czapliński (1956) basing himself on the examination of *Hymenolepididae* of birds, considers the length of the strobila and the number of segments to be "plastic features". It seems however that this problem cannot be generalized. In the course of my examinations I noticed that there exist species when the length of the strobila and the number of its segments is stable and show minimal deviations (i. e., *Hymenolepis stefańskii* Żarnowski, 1954 or *Pseudodiorchis kampinosi* Rybicka, 1958). Here we also meet a regularity already observed in the analysis of other features — a constant number of segments appears in very small species of about 1 mm length. And the smaller the number of segments the smaller is the variability. I did not meet with such species (Rybicka, 1958a) in brids and neither did Czapliński (1956), but they appear quite often in small mammals.

One more feature is connected with the stabilization of the number of segments — namely the appearance of definite organs in defi-

nite successive segments behind the scolex. This appears to be the case in such species as *Hymenolepis stefańskii* Żarnowski, 1954 or *Pseudodiorchis kampinosi* Rybicka, 1958.

Another feature connected with the general shape of the strobila is its division into several parts including equally developed segments. We observe this in the case of small tapeworms as well (*Ditestolepis, Soricinia*) occurring in *Insectivora*. The features mentioned above appear in species with different types of scolex armature as well as testes number, i. e. with characters which may be considered as a distinct indication of phylogenetic relationship, or the lack of it. It seems therefore that such features, as a constant number of segments or serial type of strobila structure, are strictly specific characters, which arose as the result of adaptation to environment.

The shape of the segments, the ratio of length to the width is usually considered as a variable feature (particularly as in the examination of preparations, there may appear some differences depending on the method of fixation used).

A knowledge of a great number of living specimens *Diorchis inflata* (Rud.) and *D. brevis* Rybicka, parasitizing *Fulica atra*, contrary to the data resulting from previously performed mass mesaurements of fixed specimens (Rybicka, 1957a) shows that the general shape of the strobila and that of the segments of both these species is so different, that in spite of these small total dimensions they can be distinguished from the point of view of this character, with the naked eye without the help of a microscope or magnifying glass.

It should be stressed that in the given example the shape of the segment constitutes a specific character of the species. The previously mentioned two species of the genus *Diorchis* show a very close relationship as far as their structural character and biology is concerned.

A separate problem is the biology of tapeworms and their relationship to their hosts. The specificity of various species of tapeworms in relation to their intermediate as well as definitive hosts is generally considerable and closely limited, which even caused students to formulate so-called parasitogenic rules (for instance Fuhrmann rule).

It seems to me however that a comparison of the phylogenic development of the tapeworms with the main directions of the phylogenic development of their hosts may help only in defining the main trend

of development of the parasites. On the other hand we cannot draw too broad conclusions concerning such taxonomic categories as genera on the basis of the relationship of particular species of parasites to various species of hosts.

Spassky (1951) stressed that the metacestodes of the family *Hymenolepididae* develop in completely different groups of intermediate hosts (*Crustacea, Insecta, Myriapoda, Oligochaeta,* and *Mollusca*) and preserve the basic features of structure and character of cysticercoids, which affirm the already mentioned stability in the structure of the larvae.

As far as the relation of the tapeworms to their definitive hosts is concerned it is necessary to quote the opinoin of Dubinina (1953) who drew attention to the fact that the essential factor having an influence on the invasion of the definitive hosts by similar parasites is not their relationship, but the common food and ecology.

Of course the development in various, sometimes remote groups of definitive hosts may have a significant influence on the tapeworm's adaptation, leading to speciation. Therefore we cannot consider the sole connection with various definitive hosts as an indicator of genus differentiation.

One more question is, whether, on the basis of the accepted theory of the secondary nature of the intermediate host, it is correct to consider the structure of early stages of development as a phylogenetic indication. It seems however, that the similarity of structure in the metacestode of various species belonging to the same family shows, in spite of their later adaptations to various intermediate hosts, that the internal morphological structure of the metacestode is a character phylogenetically stabilized and subject to relatively small changes under the influence of habitat. I think that these remarks affirm the correctness of the theory that, during the classification of tapeworms, it is necessary to take into consideration the appropriate features of adult specimens, and in addition the structure of the embryo, oncosphere, metacestode, and ontogenic development.

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STRESZCZENIE

Autorka rozpatruje na wstępie opracowany przez S p a s s k y'ego (1954) układ systematyczny tasiemców z rodziny *Hymenolepididae*, występujących u ssaków. Założeniem S p a s s k y'ego było stworzenie systemu opartego nie na pojedynczych cechach, ale na całym zespole cech, zarówno biologicznych jak i morfologicznych. W praktyce jednak, ze względu przede wszystkim na brak wielu danych dotyczących biologii tasiemców, kryteria te nie zostały w systemie S p a s s k y'ego zrealizowane, natomiast przyjęte przez niego kryteria wyodrębniania większych jednostek systematycznych (rodzajów, trybu) nasuwają szereg zastrzeżeń. Najważniejsze z nich to:

1. Wyróżnienie bardzo dużej liczby jednogatunkowych rodzajów w oparciu o bardzo niejednorodne kryteria taksonomiczne (w większości przypadków cechy, które można raczej uznać za specyficzne modyfikacje gatunkowe).

2. Przyjęcie typu układu jąder jako głównego kryterium odróżniającego nieliczne (3 spośród czterech) rodzaje wielogatunkowe.

3. Wyróżnienie tribus *Ditestolepea* w oparciu o typ budowy strobili, obejmującego gatunki różniące się nawet tą cechą, a ponadto różne pod względem cech takich, jak haki i liczba jąder.

Następnie autorka przechodzi do rozpatrzenia jakie kryteria taksonomiczne powinny być brane pod uwagę przy tworzeniu systemu, który stanowiłby odbicie stosunków filogenetycznych wśród tasiemców. Uwagi autorki dotyczą głównie rodziny *Hymenolepididae*. Przeprowadza ona analizę poszczególnych cech morfologicznych tasiemców na tle ich rozwoju filogenetycznego, w oparciu o prawo biogenetyczne Haeckela i prawo Baera. Wydaje się, że to ujęcie, w zestawieniu z danymi dotyczącymi innych grup tasiemców i podjęciem dyskusji na szerszej płaszczyźnie, będzie mogło w jakiejś mierze przyczynić się do wyjaśnienia szeregu problemów związanych z systematyką tasiemców.